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SEXUAL SELECTION IN PHOLCID SPIDERS (ARANEAE, PHOLCIDAE): ARTFUL CHELICERAE AND FORCEFUL GENITALIA

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ABSTRACT. Two aspects of pholcid reproductive biology are reviewed and appear best explained by sexual selection by female choice: the rapid and divergent evolution of male chelicerae (and clypei in some groups) which contact the female epigynum during copulation and probably act as copulatory courtship devices; and the often exceptionally strong pedipalps in males, which possibly function in correlation with the 'valve' in the internal female genitalia.

The last decades have seen a promising increase of studies examining spider reproduction from an evolutionary perspective (review: Elgar 1998). In most cases, the mechanisms of sexual selection in spiders are much the same as those documented in insects and other major groups (see e.g., Eberhard 1996, where almost every spider example used to document a specific mechanism of cryptic female choice is accompanied by at least one insect or mammal example). Some details, however, make spiders either especially useful (e.g., the pairedness of genitalia for studies of fluctuating asymmetry - Huber 1996b), or especially interesting (e.g., the apparent lack of both muscles and nerves in the male intromittent genitalia - Eberhard & Huber 1998). (For further, though less unique, spider characteristics, see Elgar 1998.)

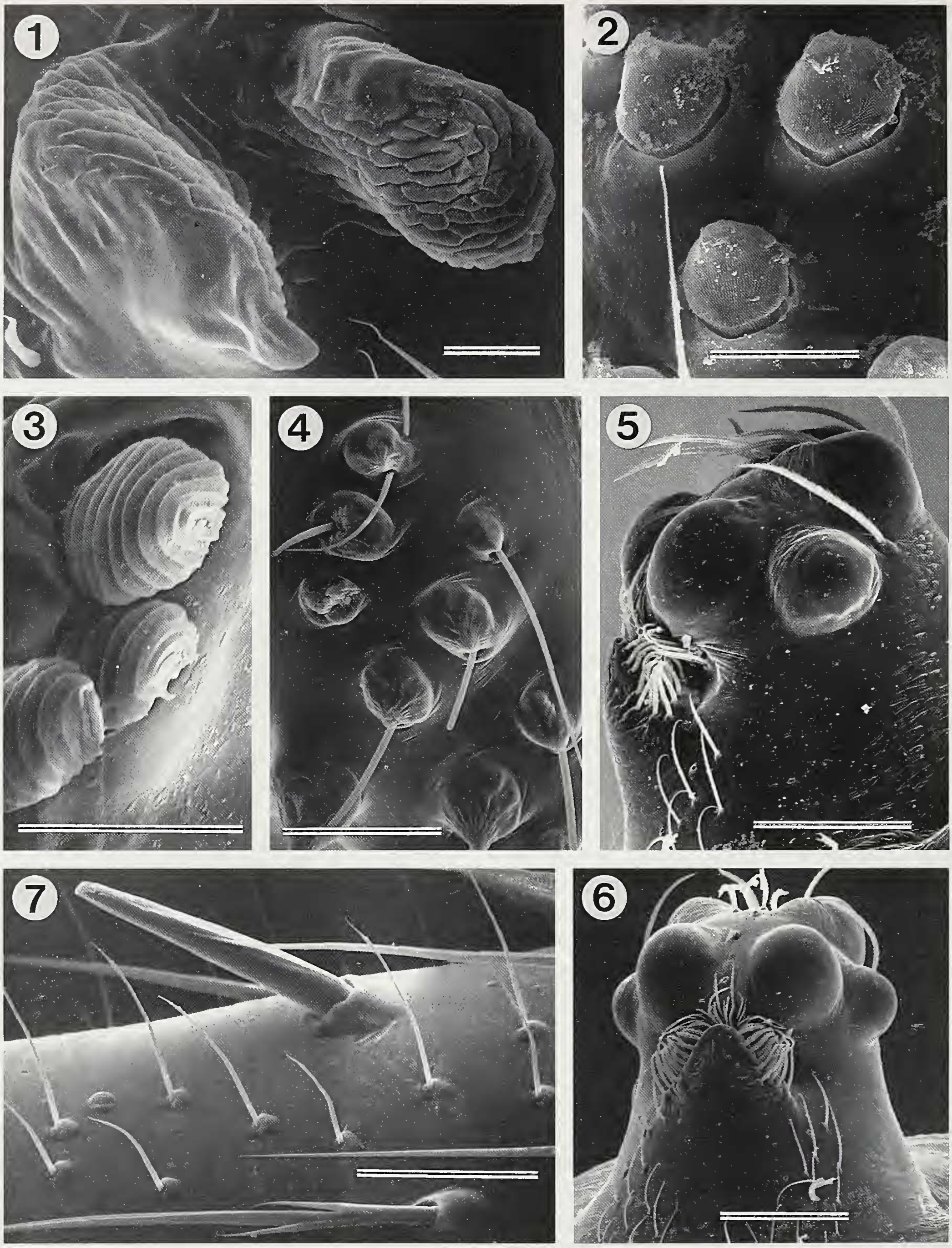
In the present paper I will briefly review some recent advances in one particular spider family, the pholcids. Pholcids are the only non-entelegyne spiders whose reproductive biology has been carefully studied in several species (Eberhard 1992; Eberhard & Briceño 1983, 1985; Huber 1994, 1995, 1996a, b, 1997a, b, 1998a, b, c; Huber & Eberhard 1997; Kaster & Jakob 1997; Uhl 1993, 1994; Uhl et al. 1995; Yoward 1998). Further advantages for the study of sexual selection are the number of synanthropic species that are available worldwide and readily maintained in the laboratory for in depth single-species studies, and a rich and diverse (mainly tropical) fauna for comparative studies.

For reasons of space, I will focus on two particular aspects: on non-genitalic contact structures which appear to evolve under selection similar to that acting on genitalia, and on the unusual phenomenon of copulatory courtship associated with vigor.

Voucher specimens of all unnamed species are deposited at the American Museum of Natural History, New York, and labeled with an I.D. number ("B.A.H. 1999 I.D.# 1–6").

ARTFUL CHELICERAE

Pholcids are not unique in having species-specific copulatory contact structures (Eberhard 1985). However, pholcids are unique, at least among spiders, with respect to the wide range of non-intromittent male structures that are sexually modified (practically the entire palp is sexually dimorphic in most pholcids, including coxa and trochanter). Two male structures deserve special attention: the chelicerae and the clypeus. At least one of them contacts the female during copulation in all species studied (Huber 1994, 1995, 1997b, 1998b; Huber & Eberhard 1997; Uhl et al. 1995), and the chelicerae in particular are often the most species-specific and taxonomically useful structures. Modifications range from hairs of different shapes to cones, rounded, pointed, hooked and blade-shaped apophyses, and even to sexually dimorphic fangs (Figs. 1–4, 10, 11, 13, 14). Several hypotheses might explain this phenomenon: (1) reproductive isolation hypotheses (lock-and-key and genitalic recognition - reviewed in Eberhard 1985); (2) the "conflict of interest hypothesis" (Alexander et al. 1997); (3) sexual selec-



Figures 1–7.—Sexually dimorphic structures in male pholcids, SEM. 1. Cheliceral apophyses in *Uthina* sp. (I.D. #1); 2. Modified hairs on the chelicerae of *Modisimus dominical* Huber; 3. Modified hairs on the chelicerae of *Spermophora senoculata* (Dugès); 4. Sclerotized cones on the chelicerae of *Physocyclus guanacaste* Huber; 5–6. Eye turret of *Modisimus culicinus* (Simon), in lateral and frontal view, showing frontal lobe; 7. Femur of *Modisimus tortuguero* Huber, showing a spine, a "normal" tactile sensillum, and several almost perpendicular hairs that cover the femora of only male walking legs. Scale bars: 0.01 mm (1–3); 0.05 mm (4, 7); 0.1 mm (5, 6).

tion by male-male competition (Eberhard & Briceño 1985); (4) the "sperm holder hypothesis" (Brignoli 1973); (5) sexual selection by female choice (Eberhard 1985, 1996).

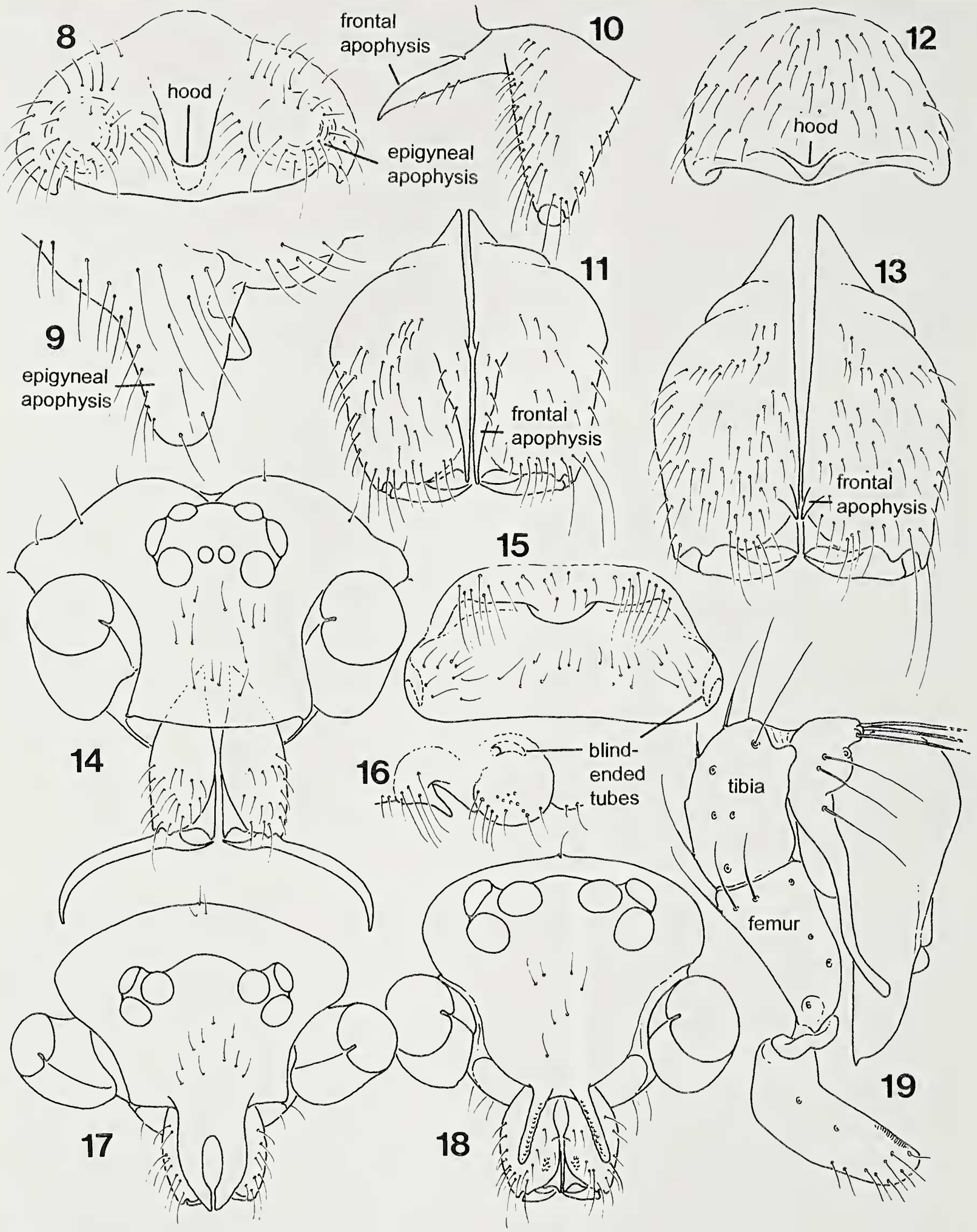
Reproductive isolation hypotheses assume that species-specific differences in pholcid chelicerae evolved because they prevent hybridization. The lock-and-key version does this on a mechanical level, the genitalic recognition hypothesis on a sensory level. Both seem unlikely to account for the phenomenon in a general way. Often there is no female "lock", for instance in most *Modisimus* species where the epigynum against which the male chelicerae are pressed during copulation is just a flat plate, but the chelicerae are nevertheless species-specific (Huber 1998a). Even in cases with a lock-and-key like fit, the hypothesis that such fit evolved to avoid cross-specific pairings is dubious because natural selection should favor early species recognition (Eberhard 1985, and references therein). However, transitory selection on cheliceral morphology in a species-isolation context cannot be ruled out, and may have been important in the past (Shapiro & Porter 1989).

The "conflict of interest hypothesis" (Alexander et al. 1997), applied to pholcid chelicerae, would explain their often complex and species-specific design by physical coercive mating during which the male has to overcome female resistance and for this purpose uses his cheliceral modifications. One prediction is that one sex (usually the male) changes to increase the match and the other sex evolves to either decrease it or it does not evolve at all in that context (Alexander et al. 1997, p. 5). The data available for pholcids do not support this scenario. To the contrary, female epigyneal structures usually appear either neutral (flat plates) or even cooperative (hoods, grooves, pits, scapes) in that they help the male to lodge his chelicerae and thus to position his body correctly. It should be emphasized that conflict per se is of course not a distinguishing characteristic between the "conflict of interest" and the "female choice" hypotheses. Conflict is a necessary result of female choosiness, and some morphological details reflect this conflict particularly clearly: in a Peruvian pholcid (I.D. #2) the male presumably (judging by male and female morphology) lodges his cheliceral apophyses into a hood in the female epigynum. However, the epigynum also carries a large apophysis on each side of the hood (Figs. 8, 9), so that only males with exceedingly long cheliceral apophyses can reach the hood (Figs. 10, 11). Thus, "genitalic arms races" of this sort may reflect selective female cooperation (the female provides a hood for those males able to overcome her obstructive apophyses) rather than female resistance to coercive males. Revealingly, the females of several putative close relatives have the cooperative structure (the hood) but not the barrier (the apophyses) (Fig. 12). Accordingly, their males' cheliceral apophyses are rather inconspicuous (Fig. 13), but nevertheless species-specific in form.

Male-male competition is equally unlikely to provide a general explanation (Huber 1994). In most species the modifications seem highly inefficient for combat, and in some cases where their shape might suggest such a function (as in the Ecuadorian pholcid illustrated in Fig. 14; I.D. #3) the female morphology strongly indicates their use during copulation (the epigynum is unusually broad and at the lateral extremes provides two blind-ended cuticular tubes, whose location and spacing indicates that they are used to accommodate the male fang-apophyses: Figs. 15, 16). However, inter- and intrasexual functions are not mutually exclusive, and fighting with chelicerae must be considered a possibility in single cases.

Brignoli's (1973) speculation that pholcid chelicerae may function to hold the sperm during sperm uptake is probably based on the observations of Gerhardt (1921–1933, references in Huber 1998d) that pholcid males make no sperm webs but transfer the drop of sperm to the chelicerae and take it up from there. This hypothesis obviously fails to explain why males should evolve such a variety of modifications to perform the same simple task of holding a drop of sperm.

Thus, by elimination, the hypothesis that seems to fit the available data best is cryptic female choice (as also for many other non-genitalic male contact structures - Eberhard 1985). Much like genitalia, chelicerae may function as copulatory courtship devices, whose elaborate morphology is used to stimulate or fit the female in a way that increases the male's chances of fathering her offspring. In this hypothesis two main factors account for the diversity and relatively rapid evolution



Figures 8–19.—Characters discussed in the present paper. 8–9. Epigynum of a Peruvian pholcid (I.D. #2) in ventral and lateral (anterior side on left) view, showing the median hood and the lateral apophyses; 10–11. Male chelicerae of the same species, lateral and frontal view; 12–13. Epigynum, ventral view, and male chelicerae, frontal view, of '*Blechroscelis*' cyaneotaeniata (Keys.); 14. Portrait of an Ecuadorian species (I.D. #3), with modified fangs; 15–16. Epigynum of the same species, in ventral and lateral (anterior side on left) view, showing the blind-ended tubes into which the male apophyses are presumably inserted during copulation; 17–18. Clypeal modifications in two *Metagonia* species from Peru (17; I.D. #4) and Brazil (18; I.D. #5); 19. Right pedipalp of a Bolivian species (I.D. #6), in which the patella is reduced. Drawn to different scales.

of male chelicerae: the unpredictability of female criteria and the never ending competition among males for access to female eggs. How females evaluate the minimal differences among conspecific males' chelicerae, i.e., the sensory and neuroanatomical basis for doing so, remains an open question.

Sexual modifications of the male clypeus are less common in pholcids, but have apparently evolved several times convergently (e.g., in *Metagonia*: Figs. 17, 18, *Holocneminus* - Huber 1997b, Deeleman-Reinhold 1994). Like the chelicerae, the clypeal modifications are highly species-specific and in one species (*Metagonia rica* Gertsch 1986) it has been shown that they also contact the female genital area during copulation (Huber 1997b).

A special case of non-genitalic contact structure is the frontal lobe in male *Modisimus culicinus* (Simon 1893) (Figs. 5, 6). Clypeal glands open at the lobe, and during copulation the female mouth is in contact with the lobe, suggesting gustatorial courtship (Huber 1997a). However, the nature and function of the gland products are unknown (trigger female responses that are favorable to male? - signal the female that copulation has occurred? - nourish the female?) meaning that a decision between natural and sexual selection is not yet possible (see Eberhard 1996 for arguments linking sexual selection and male seminal products).

FORCEFUL GENITALIA

It has been noted that "details of copulatory courtship often seem to have little relationship to male size or vigor" (Eberhard 1997: 35). If this is the rule, then many pholcids might be exceptional: their genitalia are obviously their strongest organs (provided with the largest muscles), and in *Physocyclus globosus* (Tacz. 1873) this force is apparently used to rhythmically squeeze parts of the female genitalia during copulation (Huber & Eberhard 1997). Moreover, a morphometric study of genitalic and non-genitalic structures in the same species also apparently supported the notion that there is sexual selection on male vigor: fluctuating asymmetry (FA: deviations from perfect bilateral symmetry that are thought to reflect the degree of developmental stability) in large (strong) genitalia tended to be lower than in small genitalia (Huber 1996b). In the recent literature on FA such a negative regression of FA on size is often interpreted as evidence for handicap models of sexual selection, in which only genetically "good" males can produce display structures that are both large and symmetric (Møller & Pomiankowski 1993; Watson & Thornhill 1994).

From a mechanical point of view, the pholcid male pedipalp works like a clamp, with the most distal segment (cymbium with procursus) acting against the femur. The economy of such a clamp is decreased by the two segments in-between (patella, tibia) and could be improved by elimination of one or both segments. In fact, in many pholcids (e.g., in *P. globosus*), the patella is functionally reduced in that part of the muscles of the femur insert in the tibia (Huber & Eberhard 1997) and not as usually in the patella (Ruhl & Rathmayer 1978). And in at least one species (sp. n. from Bolivia; I.D. #6) the reduction is complete, with the femur directly articulating with the tibia and no external trace of the patella left (Fig. 19). Yet another characteristic apparently functioning to increase the force applied to one critical point is realized in *P. globosus* (and probably in all *Physocyclus* species and in *Artema atlanta* Walckenaer 1837): the procursi are locked to each other, but the tip of only one is inserted into the female, moved by the muscular power of both pedipalps (Huber & Eberhard 1997).

Thus, there seems to be an ultimate advantage for males with strong palps, but the proximate function of this vigor is poorly understood. A possible solution may be in a structure of the female genitalia that is apparently unique to pholcids: the so-called "valve", an often complex "three dimensional zipper" between copulatory pouch (uterus externus) and oviduct (uterus internus). An apparent correlation has been documented between the strength and complexity of the "valve" and the strength of the male pedipalp (Huber 1998c). The correlation may be phylogenetically biased, however, so it is difficult to interpret.

It is not surprising that the recently intensified research on pholcids has raised more questions than it has answered. Thus, I would like to close this short review with yet another riddle. The males (but not females) of most species of several mainly Central American genera have the femora of their walking legs covered with short, almost perpendicular hairs

(Huber 1998a), resembling taste hairs (Foelix & Chu-Wang 1973) (Fig. 7). Nothing is known of these hairs, apart from the approximate systematic and geographical distribution of the character, the improbability of taste hairs being concentrated on femora, and the apparent lack of terminal pores necessary for chemosensory function.

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